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AFFINITIES OF THE GENUS EQUISETUM.

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THE genus *Equisetum*, as the survivor of an ancient race, which has otherwise completely disappeared, is of peculiar interest to the botanist. It is not strange that numerous attempts have been made to trace its history, and to determine its relationships to the other pteridophytes, recent and fossil.

The existing species of *Equisetum*, about twenty-five in number, are distributed over nearly the whole world — Australia alone, among the larger bodies of land, has no species in its flora. Some species, *e. g.*, *Equisetum arvense*, have a very wide range, while others, like *Equisetum giganteum*, are confined to a smaller area. The genus is sometimes subdivided, but the differences are of minor importance, and more commonly all the species are relegated to the single genus *Equisetum*.

There is a general agreement in the anatomical structure, perhaps the most marked difference being the variation in the relation of the endodermis to the vascular bundles. Thus, in certain species, like *Equisetum telmateia*, the ring of vascular bundles in the internodes is surrounded by a common outer endodermis, while in others, *e. g.*, *Equisetum hiemale*, each strand has its own sheath; while in a third type, represented

by *Equisetum silvaticum*, there is an inner as well as an outer endodermis, common to the whole circle of bundles. Other differences are the presence or absence of branches at the nodes, and the development in certain species, like *Equisetum arvense*, of special sterile and fertile shoots.

FOSSIL EQUISETALES.

The earliest fossils belonging to the Equisetales belong to the genus *Archæocalamites*, which in many respects was very similar, as regards both its anatomy and fructification, to the genus *Equisetum*. Fossils of undoubted equisetinean affinities abound in the later Palæozoic formations, being especially abundant in the coal measures. Of these, the genus *Calamites* was especially conspicuous. These were much more highly organized than the living *Equiseta*, which more nearly resemble the more ancient *Archæocalamites*. Fossils closely allied to the genus *Equisetum* occur frequently, however, in later formations, being abundant in the earlier secondary rocks.

Undoubtedly related to the Equisetales was the characteristic Palæozoic group of *Sphenophyllales*, but there is a good deal of diversity of opinion as to the possible connection of the *Sphenophyllales* with other groups of pteridophytes besides the Equisetales.

The genus *Equisetum* has been the subject of repeated investigation, and we are now well informed concerning pretty much all its structural details and developmental history. The conclusions drawn from a study of these data by different observers, however, are by no means all in accord. This difference is especially marked in the attempts to decide the affinities of the Equisetales with the other pteridophytes. It is mainly for the purpose of examining and comparing these divergent views that the present paper has been prepared.

Briefly stated, the following are the different views held as to the relationships of the Equisetales :—

1. They are allied to the lycopods.
2. They are allied to the ferns.
3. They are allied to neither of the other existing classes of pteridophytes, but have had an independent origin.

The first view has been strongly advocated by Scott¹ in England, who bases his conclusions upon a study of the fossil forms. In America, Jeffrey² has brought forward arguments in favor of the same view, from a study of both the gametophyte and sporophyte. He goes so far, indeed, as to propose a special division of the pteridophytes into the Lycopsidea, and Pteropsida, the former including both Equisetales and lycopods, the latter the ferns.

As he has presented his arguments in very clear form, it may be well to consider them somewhat in detail, to see how they will stand the test of closer examination.

From a study of the gametophyte of *Equisetum*,³ Jeffrey concludes that it most nearly resembles the gametophytes of such species of *Lycopodium* as *Lycopodium cernuum* or *Lycopodium inundatum*. "There are in both cases, the upright fleshy axis, and the same characteristically numerous lateral lobes. The archegonia of *Equisetum* and *Lycopodium* are, moreover, alike, in that in both genera they are uniformly without the basal cell, which is found without exception in the archegonia of all the isosporous Filicales" (*loc. cit.*, p. 186). He finds also that the neck canal cell is divided vertically as in *Lycopodium phlegmaria*, instead of transversely as is the case in the ferns.

Finally, in the embryo of *Equisetum hiemale* and *Equisetum limosum*, Jeffrey thinks that all the organs of the young sporophyte, including the primary root, develop from the upper or epibasal half of the embryo, in this respect also, showing a resemblance to the Lycopodiales.

The points in which the adult sporophytes of *Equisetum* and *Lycopodium* agree, are the highly developed axis, and small leaves; the development of a strobilus, and the so-called "cladosiphonic" vascular cylinder, or stele. It is on the basis of these resemblances that Jeffrey proposes the establishment of his micro-

¹ *Studies in Fossil Botany* — as well as many special papers.

² 1. The development, structure and affinities of the genus *Equisetum*. *Mem. Boston Soc. Nat. Hist.*, 1899; 2. Structure and development of the stem in the Pteridophyta and Gymnosperms. *Phil. Trans. Royal Soc.*, series B, vol. 195, 1902.

³ Jeffrey, 1, p. 186.

phyllous and cladosiphonic Lycopsidea, opposed to the megaphyllous, phyllosiphonic Pteropsida.

In his comparison of the gametophyte of *Equisetum* with that of *Lycopodium*, Jeffrey has overlooked a radical difference, to which Göebel¹ has called attention, and which has been noted by other investigators. In the former genus, the gametophyte is dorsiventral, as it is in the ferns, and the archegonia originate

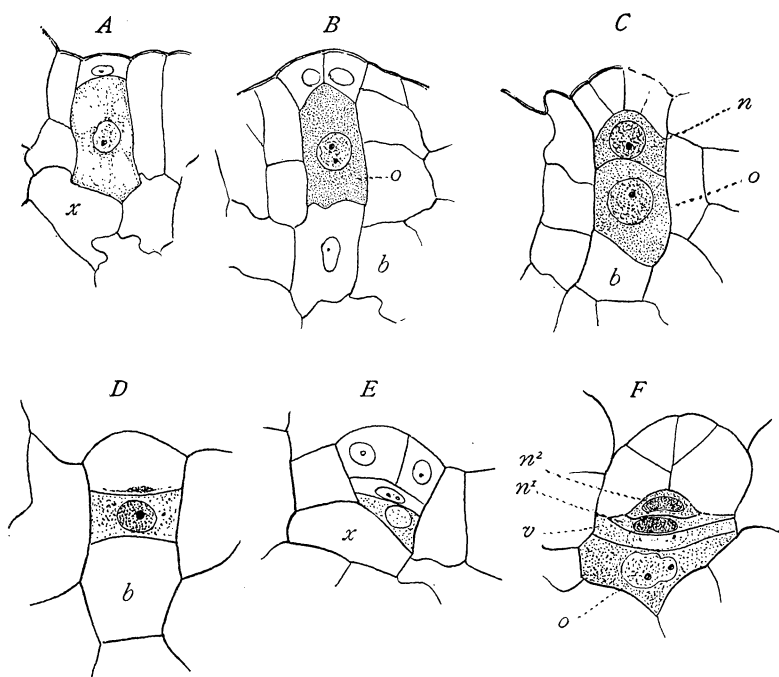


FIG. 1. — A-C, young archegonia of *Marattia douglasii*; D-F, young archegonia of *Equisetum telmateia*; b, basal cell; x, basal cell cut off before the isolation of the mother cell of the archegonium.

upon the ventral or shaded surface, the more or less conspicuously upright position being dependent upon light. The position of the archegonia upon the upper side of the prothallium is a secondary condition.

In *Lycopodium* the prothallium is radially constructed, the lobes being arranged equally about the upper part. The growth

¹ *Organographie der Pflanzen*. Zweiter Theil, Heft II, p. 409.

is marginal, and the meristem completely surrounds the upper part of the thallus, there being no proper apical growth as in *Equisetum*.

The gametophyte of *Equisetum* can much more properly be compared with that of the lower ferns like *Osmunda* or *Marattia*,

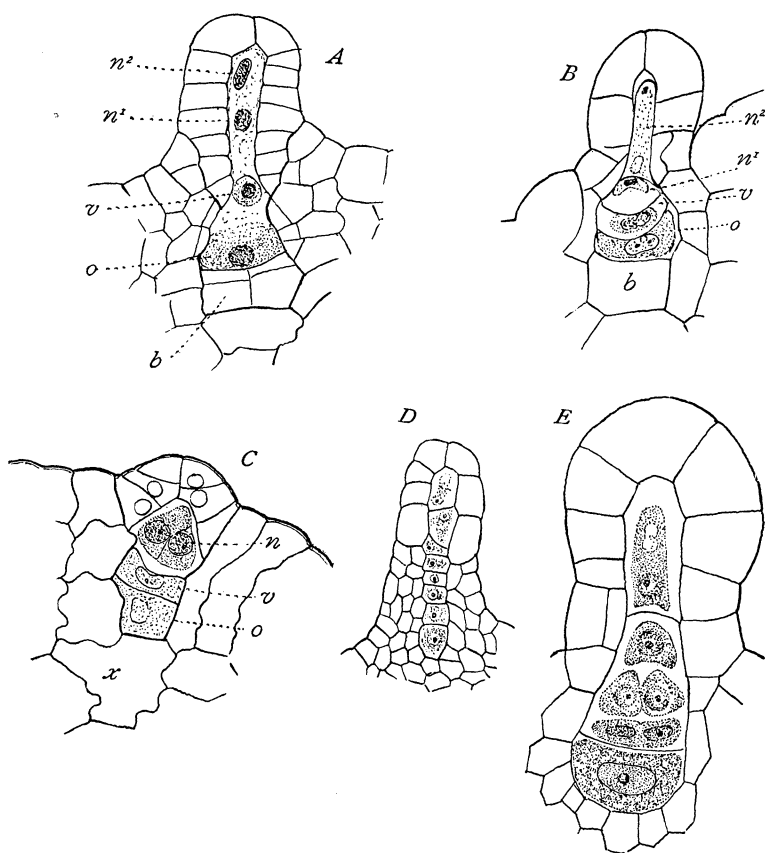


FIG. 2. — A, archegonium of *Botrychium virginianum*; B, *Equisetum telmateia*; C, *Marattia douglasii*, showing longitudinal division of the neck canal cell; D, *Lycopodium clavatum*; E, *Lycopodium phlegmaria*; b, basal cell; o, egg cell; v, ventral canal cell; n, n', neck canal cells. (D, after Bruchmann; E, after Treub.)

and in the former genus especially there are sometimes developed lobes not essentially different from those found in the gametophyte of *Equisetum*.

As to the presence or absence of the basal cell of the arche-

gonium, this is probably not a point of fundamental importance. The writer has taken the trouble to examine this point somewhat carefully in *Equisetum telmateia*, *Marattia douglasii*, and *Osmunda cinnamomea*. In the former, an unmistakable basal cell was found in several instances (Fig. 1, *D*), although there is no question that ordinarily it is absent. Jeffrey states that in the species examined by him, it is universally wanting. In *Marattia* it was generally present, but much less conspicuous than in most ferns. Not infrequently, however, it was entirely wanting, as according to Jonkman (*Bot. Zeitung*, 1878), it is in the species of *Marattia* examined by him. Farmer says that in *Angiopteris* it is also absent.¹ In *Osmunda cinnamomea*, while ordinarily present, it may be wanting.

It is thus evident that too much stress cannot be laid upon the presence or absence of the basal cell. It is probably no more important than the pedicel in the archegonium of the Marchantiaceæ. *Marchantia polymorpha*, for instance, regularly develops such a pedicel cell, while in *Targionia* and *Fimbraria*, it is regularly absent, and the archegonium is closely sessile.

An interesting condition was noted in several cases in *Equisetum* (Fig. 1, *E*) where a basal cell was developed before the final cutting off of the mother cell of the archegonium. An exactly similar case was found in *Marattia* (Fig. 1, *A*).

Jeffrey has described a peculiarity in the archegonium of *Equisetum* which he thinks points to a relationship with *Lycopodium* as in one species, *Lycopodium phlegmaria* (Fig. 2, *E*), a similar condition has been found. This is the longitudinal division of the neck canal cell. To judge from my own preparations of *Equisetum telmateia*, this rarely occurs in that species, where the division wall is normally transverse, as it is in the ferns (Fig. 1, *F*), and most other Archegoniates. A similar longitudinal division has been observed in species of *Isoetes*.² In one instance a similar longitudinal division was found in *Marattia* (Fig. 2, *C*).

To summarize: it seems to the writer that in all respects

¹ *Annals of Botany*, vol. 6, 1892.

² Arnoldi, *Bot. Zeit.*, 1896; Lyon, *Bot. Gazette*, 1904.

there is decidedly more resemblance between the gametophyte of *Equisetum* and that of the lower ferns than there is between it and any species of *Lycopodium*.

THE EMBRYO.

According to Sadebeck,¹ who has made a special study of the embryo of *Equisetum*, the primary or basal wall of the embryo, which is transverse, divides the embryo into an upper or epibasal cell, and a lower or hypobasal one. From the epibasal cell is derived the apex of the shoot; from the hypobasal one the foot and the primary root. My own studies upon *Equisetum telmateia*, although not complete, confirm Sadebeck's statement. Jeffrey² thinks it doubtful whether the root in *Equisetum hiemale* and *Equisetum limosum* originates from the hypobasal region of the embryo, but to judge from his figures 7, 8, it is by no means certain that his interpretation is correct. While comparing the embryo of *Equisetum* with that of *Lycopodium*, in which all of the organs of the embryo arise from the epibasal half, he fully recognizes the fact of the presence of the suspensor in the lycopods, and its absence in *Equisetum*. Even if his assumption of the epibasal origin of the root were correct, it could more aptly be compared with the embryo of *Botrychium*, where he has shown³ that both root and shoot are of epibasal origin, and moreover, the cotyledon develops secondarily from the shoot as the first foliar sheath does in *Equisetum*.

THE MATURE SPOROPHYTE.

The sporophyte of *Equisetum*, as is well known, differs widely in its general structure from either the ferns or lycopods. The structural type as it exists in the living horsetails is evidently a very ancient one, and the oldest fossils belonging to the *Equisetales* are not essentially different in their structure from the living species.

¹ *Bot. Zeit.*, 1877.

² *Loc. cit.*, p. 169.

³ The Gametophyte of *Botrychium*. *Proc. Canad. Institute*, vol. 5, 1898.

The hollow jointed stem, the remarkably regular apical growth of both shoot and root, and the structure and arrangement of the vascular bundles are very different from the lycopods with which it has been attempted to connect the Equisetales. It is true that both the latter class and the lycopods are characterized by relatively small leaves, but their structure and relation to the shoot are very different in the two classes.

It may be questioned whether the excessive reduction of the leaves found in most species of *Equisetum* is not a secondary condition. The oldest known type, *Archæocalamites*, while agreeing closely in its general structure with *Equisetum*, differed in the very much better developed leaves, which not only were much larger than those of *Equisetum*, but were repeatedly branched in a dichotomous manner, more suggestive of the leaves of certain ferns than of any forms among the lycopods. Their relation to the shoot, however, was precisely that of the existing forms. The peculiar extinct order, the *Sphenophyllales*, which are admittedly of equisetaceous affinities, also possessed dichotomously divided leaves, or wedge-shaped leaves with dichotomous venation.

The fact that both Equisetales and lycopods have the sporangial structures arranged in a strobilus or cone, can hardly be taken as a necessary indication of relationship. The structure of the cones in the two classes is very different, the sporangio-phores of *Equisetum* being hardly comparable to the true sporophylls of *Lycopodium*. Moreover, true strobili are known in the fern series, as shown by the cycads, whose relationship with the ferns is now almost universally admitted.

While the structure of the sporangia and of the spores is extremely characteristic in *Equisetum*, the development of the sporangium is much more like that of the eusporangiate ferns than like that of any of the *Lycopodiinæ*.

Jeffrey lays much stress upon the arrangement of the vascular bundles in *Equisetum*, which he thinks can be compared better to those of the *Lycopodiales* than to those of the ferns. Van Tieghem,¹ on the other hand, refers *Equisetum* to his

¹ *Traité de Botanique*.

“astelic” type, to which *Ophioglossum* also belongs. Whether or not *Equisetum* is astelic in Van Tieghem’s sense, there is a very important respect in which it differs from the other pteridophytes that have been critically studied, namely, the origin of the vascular bundles from the cortical region, and not from the primary central cylinder. A longitudinal section of the shoot shows an early differentiation into a central cylinder and cortex, but it is from the latter and not from the former that the vascular strands originate, the central cylinder developing only the pith.

Jeffrey in his study of the development of the vascular system in the young sporophyte does not state whether the relation of the vascular strands to the primary central cylinder is the same as in the adult sporophyte, but there is no reason why it should be different, as otherwise the arrangement of the bundles is the same.

He states that the arrangement of the bundles in the primary shoot is the same as in the later ones, except that he finds at the base of the shoot below the first leaf sheath, a closed ring of vascular tissues, such as occurs at the nodes, and considers this as a remnant of a primitive cylindrical stele or vascular cylinder; but it is not quite clear why this does not simply represent the first node where we should expect to find essentially the same arrangement of the tissues as in the later nodes.

As in the later shoots, there extend between the nodes separate vascular strands corresponding in number to the teeth of the leaf sheaths,—three as a rule in the primary shoot. These fork at the nodes, and each branch joins one from the neighboring bundle, so that the vascular strands alternate in succeeding internodes as they do in the later formed shoots.

In *Archæocalamites*, the earliest known type, the bundles are continuous from one internode to another, but in the *Calamites* of the Carboniferous, the same arrangement is found as in *Equisetum*.

Jeffrey considers the spaces between the internodal strands as gaps in an originally continuous cylinder, comparable to the large foliar gaps found in the cylindrical stele of the ferns, or the ramular gaps, occurring where branches are given off, in the

lycopods. From a study of the fossil Equisetales, especially Archæocalamites, he concludes that these gaps are to be considered as ramular gaps, although he admits that in Equisetum they occur opposite the leaves. He proposes the term "cladosiphonic" to designate a cylindrical stele, with ramular gaps, such as he assumes for the Equisetales and Lycopodiales.

Admitting that the vascular system of Equisetum can be referred to a siphonostelic type, it is hard to see how we can reconcile Jeffrey's idea of cladosiphony with the facts. So far as we can see there is absolutely no difference in the arrangement of the bundles of the internodes and their intervening spaces in shoots which develop branches, and those which are without them. In all cases, the number of internodal strands — and, of course, that of the gaps between them — corresponds to the number of leaf traces developed from the foliar sheath. The gaps are equally present in the primary unbranched shoot, and in the densely branched sterile shoots of *Equisetum arvense* or *Equisetum telmateia*. It certainly seems hardly reasonable to suppose that an ideal branch — so to speak — could cause the development of a ramular gap, when no actual branch is present.

Jeffrey lays stress upon the fact that in Archæocalamites, the branches are really opposite the spaces between the internodal vascular strands; but it appears¹ that Archæocalamites was often very sparingly branched, but this does not seem to bear any relation to the presence of the alleged ramular gaps, which are perfectly developed whether branches are present or not.

We see no reason why we should try to reduce the vascular system in the Equisetales to either of the types found in the other phyla of pteridophytes. The peculiar character of the stem, with its hollow jointed structure, would naturally involve quite a different arrangement of the tissues. Moreover, as has already been indicated, the origin of the vascular strands is entirely different from that of the typically axial vascular cylinders of the other classes. There is no valid reason why the separate strands in Equisetum may not have existed from the

¹ Scott, *loc. cit.*, p. 65; Potonie, *Lehrbuch der Pflanzenpalaeontologie*, 1899.

first. The oldest fossils show the same type, and in the embryo, before any trace of the vascular bundles can be seen, there is developed the three-leaved primary foliar sheath, and corresponding to the three teeth of the foliar sheath, are developed simultaneously the three vascular strands of the first internode.

THE SPHENOPHYLLALES.

The Sphenophyllales are exclusively fossil forms which show evident affinities with the Equisetales, from which they differ especially in the arrangement of the tissues of the stem. Instead of the large central cavity found in the stem of *Equisetum*, *Sphenophyllum* has an axial solid vascular cylinder more like that of the modern lycopodiaceous forms than like any other existing pteridophytes.

Scott¹ considers that the Sphenophyllales are to some extent intermediate between Equisetales and Lycopodiales, basing his opinion mainly upon the anatomical characters, especially those of the stem. The peculiar fossil *Cheirostrobus*² he especially considers a synthetic type, having the sporangia of the *Equisetum* type, but the vascular system of a lycopod.

Potonie³ holds that the Sphenophyllales are an early offshoot of the equisetaceous series, perhaps directly connected with *Archæocalamites*. The characteristic triarch or hexarch bundle of the stem suggests a three-sided apical cell like that of *Equisetum*, but in the *Psilotaceæ*, which are commonly associated with the Lycopodiales, there is a somewhat similar type of stele, and these forms also have a single tetrahedral initial cell in the shoot.

One objection to considering the Sphenophyllales a synthetic type is that all the existing types of pteridophytes were clearly differentiated in formations earlier than any in which remains of the Sphenophyllales certainly occur.

¹ *Studies in Fossil Botany*, 1900.

² *loc. cit.* pp. 106-114.

³ *loc. cit.*, p. 180.

The peculiar, jointed, hollow stem, with the characteristic arrangement of the bundles, except for their alternation in succeeding internodes, is as marked in the earliest Equisetales as it is in the existing genus, and cannot readily be derived from either the type of the ferns or lycopods, both of which are clearly recognizable in the formations where they first occur. So far as we can judge from the geological record, the central solid stele of *Sphenophyllum* is a more recent development than the separated vascular strands of the typical Equisetales, as exemplified by *Archæocalamites*.

CONCLUSIONS.

As we have endeavored to show, the gametophyte of *Equisetum* resembles that of the eusporangiate ferns rather than *Lycopodium*, both in its dorsiventral character, and method of growth, and especially in the large multiciliate spermatozoids. We believe that these resemblances indicate a real, although extremely remote, relationship with the lower ferns.

The early divisions of the embryo are not unlike those in the fern embryo, but the early preponderance of the shoot, and the subordination of the leaves, very soon produce an extremely different type of sporophyte, and it is highly probable that the peculiarities of the sporophyte were established at a very remote period, and are not modifications of another type. The dichotomously divided leaves of the older Equisetales and *Sphenophyllales* are somewhat reminiscent of those of some ferns, although it is not at all likely that there is any direct genetic relationship between these.

The most probable conclusion to be reached, in view of the evidence at hand, would seem to be that the two series, the ferns and Equisetaceæ, are descended from a common stock, in which the gametophyte was not unlike that of the existing species of *Equisetum* and the lower eusporangiate ferns. It must be assumed, however, that the peculiarities of the sporophytes became established at so remote a period that one cannot say that either was derived from the other—*i. e.*, from the same ancestral stock represented by the gametophyte as it now exists

in the two classes, there arose quite independently two types of sporophyte : one distinguished by a preponderant development of the shoot, the other marked by the great development of the leaf structures.

Neither of these classes is at all related to the Lycopods, which show strong evidences of being derived independently from a very different type of gametophyte.

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